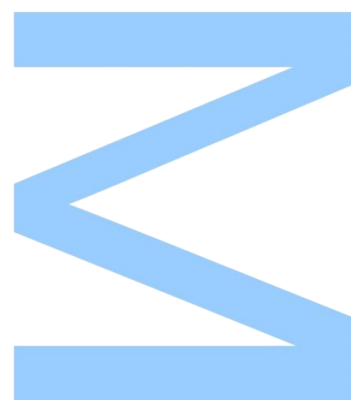
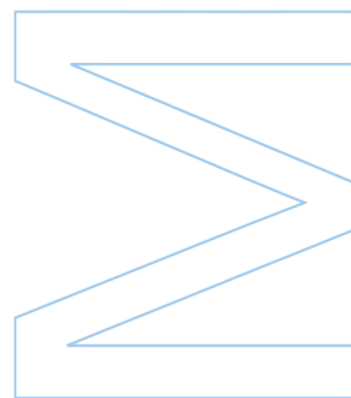


# **Spatial and temporal variation of kelp beds and associated macroalgal assemblages along the Portuguese coast**

Daniela Pinho

Master's Thesis presented to Faculdade de Ciências da  
Universidade do Porto in Ecology, Environment and Territory  
2014





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**Daniela Pinho**

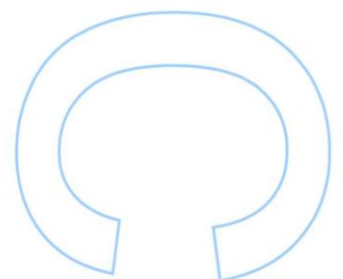
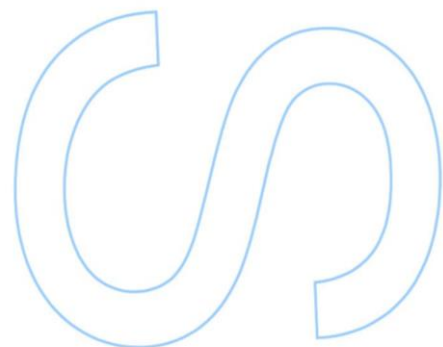
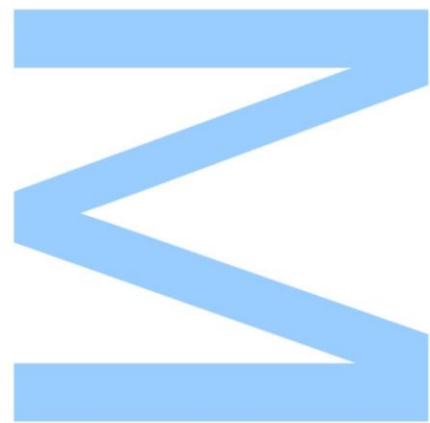
Master's degree in Ecology, Environment and Territory  
Biology Departament  
2014

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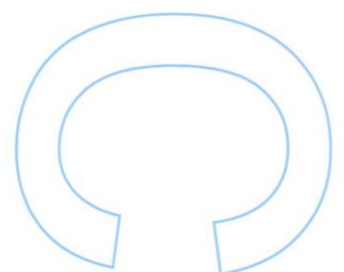
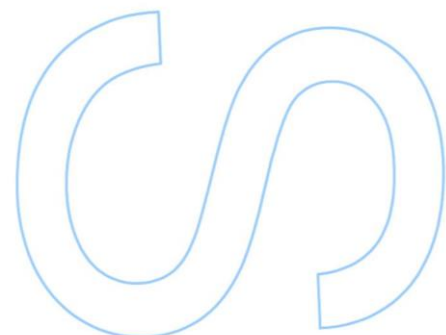
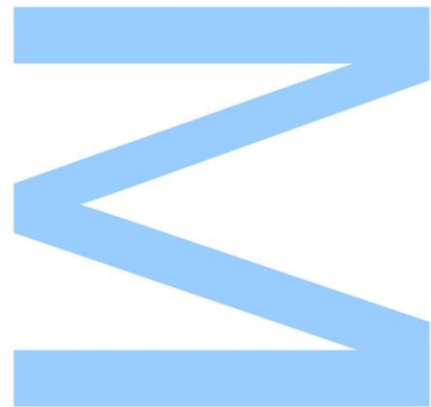
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Todas as correções determinadas  
pelo júri, e só essas, foram efetuadas.  
O Presidente do Júri,

Porto, \_\_\_\_/\_\_\_\_/\_\_\_\_



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To my parents,

## Abstract

There is evidence that kelp communities are globally declining, so it is pertinent to investigate patterns of spatial and temporal variation in the distribution and abundance of remaining populations and their associated organisms. In this study, patterns of variation of kelps and associated macroalgal assemblages were examined, three times over a period of two years, at three regions along a latitudinal gradient that encompasses a natural gradient in temperature and nutrient availability across the Portuguese coast (Viana do Castelo, Peniche and Sines, located in the north, centre and south of continental Portugal, respectively). Kelp species were mostly found at Viana do Castelo, which was also clearly separated from the other two regions in terms of algal assemblage structure. This pattern was consistent through the years, providing support to this general spatial configuration. Nevertheless, the overall richness of taxa increased towards lower latitudes. These findings indicated that kelp beds in southern European waters are currently restricted to northern Portugal, though supporting less diverse macroalgal assemblages compared to those located in central and south Portugal.

## Key words

Kelps, latitudinal gradient, algal assemblages, subtidal, spatial variability, temporal variability

## Resumo

Existem evidências de que as comunidades de kelps estão em declínio a nível global, assim sendo, torna-se pertinente investigar os padrões de variação espacial e temporal na distribuição e abundância das populações existentes assim como dos organismos associados.

Neste estudo foram examinados padrões de variação dos kelps e das macroalgas a eles associadas. Isso foi concretizado três vezes ao longo de um período de dois anos em três regiões diferentes ao longo de um gradiente latitudinal que acompanha um gradiente natural na temperatura e disponibilidade de nutrientes ao longo da costa Portuguesa (Viana do Castelo, Peniche e Sines, localizados a norte, centro e sul do continente Português respetivamente).

As espécies de kelps estiveram mais presentes em Viana do Castelo, estando esta região claramente separada das restantes em termos da estrutura da comunidade de algas. Este padrão foi consistente ao longo dos anos, providenciando suporte a esta configuração espacial. Apesar disto, a riqueza total de taxas aumentou com latitudes mais baixas. O que poderá indicar que as comunidades de kelps nas águas do sul da Europa estão restritas ao norte de Portugal, suportando uma menor diversidade de macroalgas comparando com as comunidades localizadas no centro e sul de Portugal.

## Palavras-chave

Kelps, gradiente latitudinal, comunidades de algas, subtidal, variação espacial, variação temporal

## Contents

Abstract .....	4
Key words .....	4
Resumo .....	5
Palavras-chave .....	5
List of tables .....	7
List of figures .....	8
List of abbreviations .....	9
Introduction .....	10
Materials and methods .....	12
o Study area .....	12
o Collection of data .....	13
o Analysis of data .....	14
Results .....	16
o Oceanographic patterns .....	16
o Algal assemblages .....	16
Discussion .....	26
References .....	29
Appendix .....	33

## List of tables

Table 1: Permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons .....	18
Table 2: ANOVA on the richness of algal taxa, the Pielou's evenness index and the total algal biomass .....	21
Table 3: SIMPER results.....	33
Table 4: ANOVA on SIMPER results .....	35
Table 5: Taxa distribution per region and climate affinity.....	39



## List of figures

Figure 1: Map of continental Portugal with sampling regions.....	12
Figure 2: Sampling kelps and associated macroalgal.....	13
Figure 3: Identification of taxa at the laboratory.....	14
Figure 4: Annual average of (A) chlorophyll- <i>a</i> and (B) sea surface temperature at each region .....	16
Figure 5: Total number of algal taxa at each region according to their climate affinity. 17	
Figure 6: Two-dimensional non-metric multidimensional scaling plot within each region over the three sampling years.....	19
Figure 7: Richness of algal taxa at each region.....	20
Figure 8: Biomass of algal taxa at each region.....	22
Figure 9: Biomass of individual algal species at each region and time of sampling. ....	24
Figure 10: Biomass of individual algal species at each region and time of sampling. ..	25

## List of abbreviations

ANOVA: Analysis Of Variance

CHL *a*: Chlorophyll *a*

Fig.: figure

PEN: Peniche

SIN: Sines

SNK: Student Newman Keuls

SST: Sea Surface Temperature

S. E.: Standard Error

S.R.: Species Richness

Tab.: Table

VIA: Viana do Castelo

## Introduction

Macroalgal assemblages, including large brown algae such as kelp and fucoid species, are worldwide important habitat-formers, space occupiers and food providers in nearshore temperate habitats (Schiel and Foster 1986). Kelps, in particular, are “foundation” species (*sensu* Dayton 1975) with a high ecological, social and economic value, due to their role in supplying primary production, and their ability to support diverse associated assemblages, from algae to invertebrates to fishes (Wernberg *et al.* 2010). For example, the average net primary productivity of kelp forests is around  $1000 \text{ g C m}^{-2} \text{ y}^{-1}$  (Reed and Brzezinski 2009), but it could reach values up to  $3000 \text{ g C m}^{-2} \text{ y}^{-1}$ , as described *Macrocystis* and *Laminaria* (Gao and McKinley 1994). It is estimated that one third of this production moves up into higher trophic levels through grazing (Duarte and Cebrian 1996).

As cold-water species, kelps are negatively affected by high temperatures, which can critically decrease their reproduction, growth and overall survival (Steneck *et al.* 2002; Wernberg *et al.* 2010). Despite species-specific large variations in thermal tolerance and acclimatization capacity (Biskup *et al.* 2014), kelp abundances are expected to decline with increasing temperatures under global warming (Wernberg *et al.* 2010).

The continental Portuguese coast is an interface between ‘cold’ and ‘warm’ water regions where macroalgal species of both boreal and Lusitanian origin (Southward *et al.* 1995; Lima *et al.* 2007) overlap. Many species have their southern or northern distributional range edges along this coast (Fischer-Piette and Prenant 1957; André 1971; Lima *et al.* 2007), while other species show latitudinal clines in their presence (Boaventura *et al.* 2002; Pereira *et al.* 2006;). The Portuguese coast is situated in the North Atlantic Upwelling System of the western coast of the Iberian Peninsula (Wooster *et al.* 1976; Prego *et al.* 2007). Normally, winds and ocean nearshore currents present a strong seasonal variability, with clearly distinguished summer and winter patterns. The northern and north-western prevailing winds during summer (Reis and Gonçalves 1988) are responsible for nearshore upwelling events, with concomitant nutrient inputs towards the ocean surface and so a promotion of primary productivity (Prego *et al.* 2007).

Latitudinal gradients in ocean climate, especially year-round seawater temperatures and primary production (Peliz and Fiúza 1999; Lemos and Pires 2004) have been proposed to explain the declining of some seaweed species along the

Portuguese coast. A reduction in the intensity of upwelling events has also been suggested to cause alterations in species distributions (Lima *et al.* 2006). Within this context, there is a general perception, and some empirical evidence, suggesting that kelps that once dominated the whole Portuguese coast are tending to become restricted to the northern region (Assis *et al.* 2009; Tuya *et al.* 2012).

Assessing patterns of spatial and temporal variation of macroalgae along latitudinal gradients is relevant in the context of examining their possible responses under present and predicted changing environmental conditions (Harley *et al.* 2006; Poloczanska *et al.* 2007; Wernberg *et al.* 2010, 2011). Nevertheless, such studies are scarce on the Portuguese continental coast, despite some recent advances (Assis *et al.* 2009; Tuya *et al.* 2012). This study was aimed at contributing to fill this gap by examining whether the abundance of kelp beds and the overall structure of associated macroalgal assemblages differed between three regions located along the Portuguese coast. Sampling was repeated at three times (in 2011, 2012 and 2013) to test for the temporal consistency of patterns.

## Materials and methods

### Study area

The study was conducted at three regions: Viana do Castelo (VIA, 41,5° N), Peniche (PEN, 39,2° N) and Sines (SIN, 37,8° N) (Fig. 1). The coastline is characterized by intertidal and shallow subtidal limestone, sandstone, shale or granitic reefs, interspersed within extensive sandy habitats (Tuya *et al.* 2012).

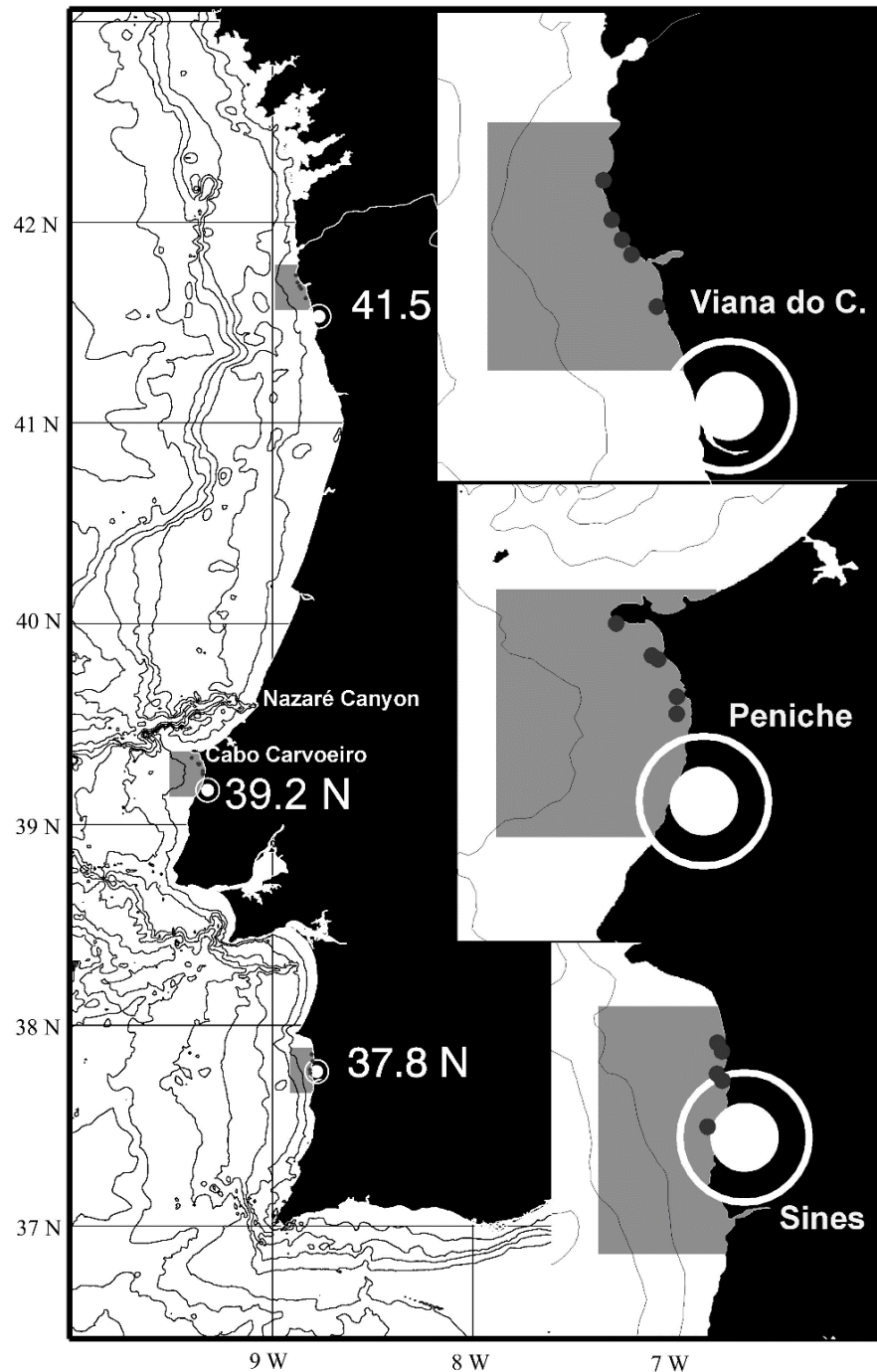


Figure 1: Map of continental Portugal with sampling regions

## ○ Collection of data

To describe the environmental conditions along the Portuguese coast, data on sea surface temperature (SST) and chlorophyll *a* (Chl *a*) were collected from satellite records over a period of 11 years (from January 2003 to December 2013). Monthly average values for each variable within each region (VIA, PEN and SIN) were acquired from MODIS-Aqua 4 km, available on the Giovanni online data system (<http://disc.sci.gsfc.nasa.gov/giovanni>), developed and maintained by the NASA GES DISC (Acker and Leptoukh 2007).

Algal assemblages were sampled in spring/summer (the period of the year when macroalgal diversity and standing stock is usually the highest), of 2011, 2012 and 2013. At each year, five reefs (several km apart, depth between 8 m and 12 m) were randomly selected at each region and six replicate quadrates (50 x 50 cm) were randomly laid out on each reef. A destructive sampling was carried out by scraping all vegetation within each quadrate (Fig. 2). Collected material was stored in separate bags, kept in sea water for transportation to the laboratory, and there immediately frozen until sorting and subsequent identification. In the laboratory, once defrosted, all samples were sorted and identified to species or, when not possible, to the genus level (Fig. 3). The biomass (fresh weight) of each taxon was measured after rinsing with freshwater and removing the excess of water by shaking and drying algal tissues with paper.



Figure 2: Sampling kelps and associated macroalgal



Figure 3: Identification of taxa at the laboratory

### ○ Analysis of data

Differences in macroalgal assemblage structure among regions were tested with three-way permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on Bray-Curtis dissimilarities calculated from untransformed data. The model included the factors: Time (three levels, random), Region (three levels, fixed and crossed with Time) and Reef (five levels, random and nested within both Time and Region). When pertinent, pairwise tests were carried out as post-hoc multivariate comparisons.

Multivariate patterns were visualized through non-metric multidimensional scaling (nm-MDS) ordination plots of centroids for each reef at each region and time of sampling, obtained as averages of principal coordinates calculated from the Bray-Curtis dissimilarity matrix of the whole set of data (McArdle and Anderson 2001). A matrix of Euclidean distances between each pair of centroids was calculated and used as the input for the nm-MDS.

The SIMPER procedure (Clarke 1993) was performed to determine the taxa most contributing to dissimilarities within and between regions. A taxon was considered important if its contribution to the total dissimilarity of that region was  $\geq 3\%$ , with a cut-off cumulative contribution established at 80%. Data on the biomass of these taxa, as well as the species richness, the Pielou's evenness index ( $J$ ) and the total algal biomass of each replicate were analysed through analysis of variance (ANOVA), based on the same design previously described. Before each ANOVA, the assumption of

homogeneity of variances was checked with the Cochran's C test. When possible, data were log-transformed to avoid heterogeneous variances. When this was not successful, untransformed data were analysed and results were considered significant at  $p < 0.01$  to compensate for an increased probability of a type I error (Underwood 1997). When relevant, Student-Newman-Keuls (SNK) tests were used for a posteriori comparisons of means. In the case of the total biomass, the non-significant (at  $p > 0.25$ ) random interaction 'Time x Region' was pooled to increase the power of the test involving the factor 'Region' (Underwood 1997).

Finally, each identified taxon was assigned to each of two bioclimatic groups: 'cold water' Atlantic boreal and 'warm water' Lusitanian species (according to Alvarez *et al.* 1988; Luning 1990; Tuya *et al.* 2012; Guiry and Guiry 2014). The proportion of 'cold water' and 'warm water' algae in each region was calculated. A third, additional, group was considered as 'widely distributed' taxa, i.e. those having wide distribution ranges.

ANOVA and SNK tests were performed with WinGMAV5 Software, and the remaining (excluding the proportion of bioclimatic groups) using Primer 6 Software & PERMANOVA+ $\beta$ 3 add-on.



## Results

### ○ Oceanographic patterns

Chlorophyll *a* (Fig. 4A) and SST (Fig. 4B) showed a clear gradient from north to south. Chl *a*, in particular, was two times higher at VIA than at SIN, with intermediate values at PEN, while the mean SST progressively increased from VIA to PEN to SIN.

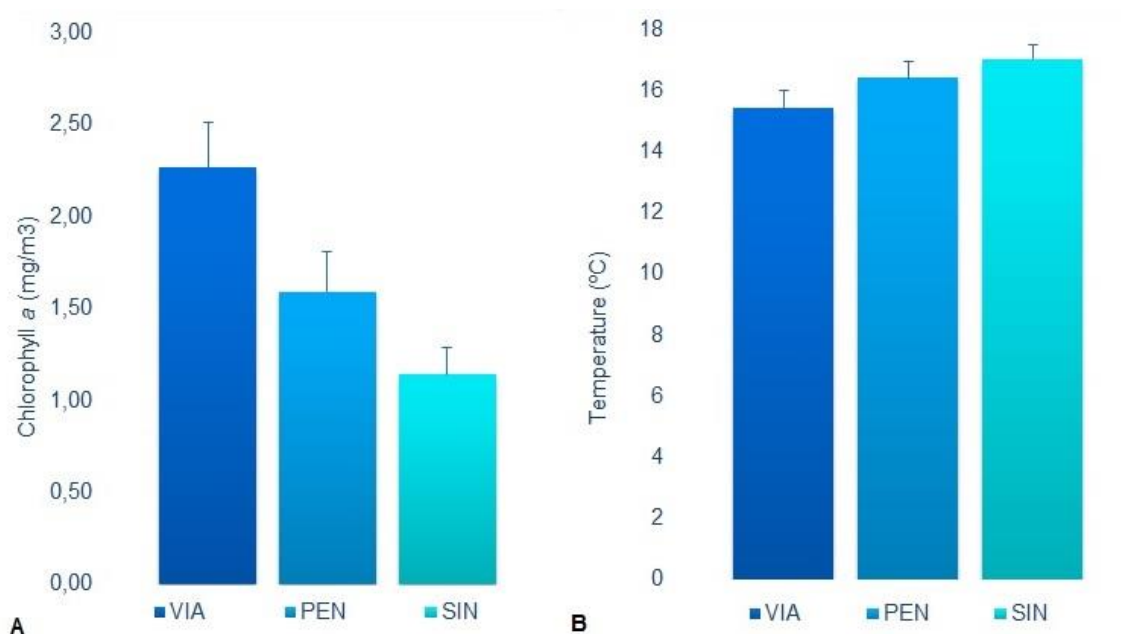


Figure 4: Annual average of (A) chlorophyll-*a* and (B) sea surface temperature at each region (n=132 months; 11 years). VIA: Viana do Castelo; PEN: Peniche; SIN: Sines.

### ○ Algal assemblages

In total, 132 species of macroalgae were identified from the 270 replicate quadrates. The main contribution was provided by Rhodophyta, with the orders Ceramiales and Gigartinales being particularly rich (36 and 11 taxa, respectively). Ochrophyta were mostly represented by Fucales and Dictyotales (5 and 4 taxa, respectively), while the order Ulvales (4 taxa) was the main contributor to Chlorophyta. When grouped according to their climate affinity, macroalgal assemblages at VIA

showed the highest proportion of ‘cold water’ species (28.1%), followed by PEN (10.9%) and SIN (7.3%). The opposite pattern was observed for ‘warm water’ species, ranging from SIN (25.6%) to PEN (19.6%) to VIA (15.6%) (Fig. 5 and Tab. 5 in the appendix).

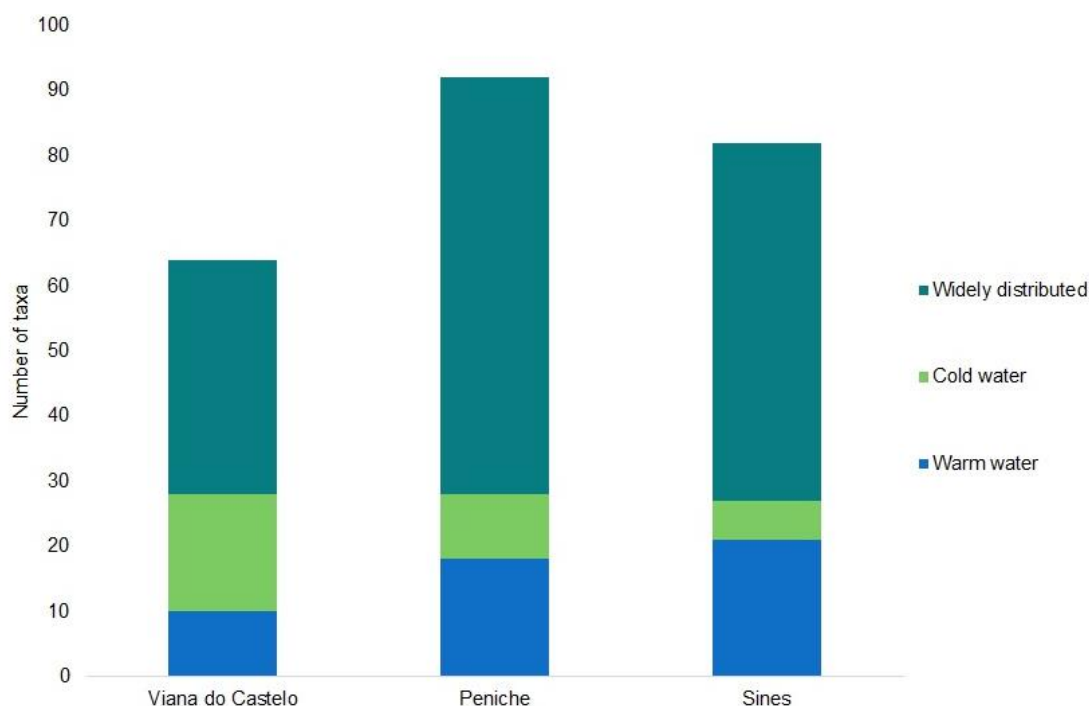


Figure 5: Total number of algal taxa at each region according to their climate affinity.

At the assemblage-level, temporally variable differences in macroalgal structure among regions were detected through a significant interaction 'Time x Region' (Tab. 1 and Fig. 6). A larger similarity between PEN and SIN, compared to VIA, was evident, particularly in 2012 and 2013 (Fig. 6).

Table 1: Permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons examining the effects of time, region and reef on whole macroalgal assemblages associated to kelp species. Significant effects are reported in bold.

Source of variation		df	MS	pseudo- <i>F</i>	p	Denominator
Time	= T	2	33337.0	3.35	<b>0.001</b>	Reef (TxR)
Region	= R	2	80513.0	3.41	<b>0.001</b>	T x R
T x R		4	23589.0	2.37	<b>0.001</b>	Reef (TxR)
Reef (TxR)		36	9937.0	5.35	<b>0.001</b>	Residual
Residual		225	1858.2			

Pairwise comparisons: T x R

	<u>2011</u>	<u>2012</u>	<u>2013</u>
VIA vs. PEN	$t = 2.577$	$t = 2.610$	$t = 1.907$
	$p = 0.001$	$p = 0.001$	$p = 0.001$
VIA vs. SIN	$t = 2.433$	$t = 1.915$	$t = 2.137$
	$p = 0.001$	$p = 0.002$	$p = 0.01$
PEN vs. SIN	$t = 1.855$	$t = 1.534$	$t = 1.693$
	$p = 0.002$	$p = 0.029$	$p = 0.01$

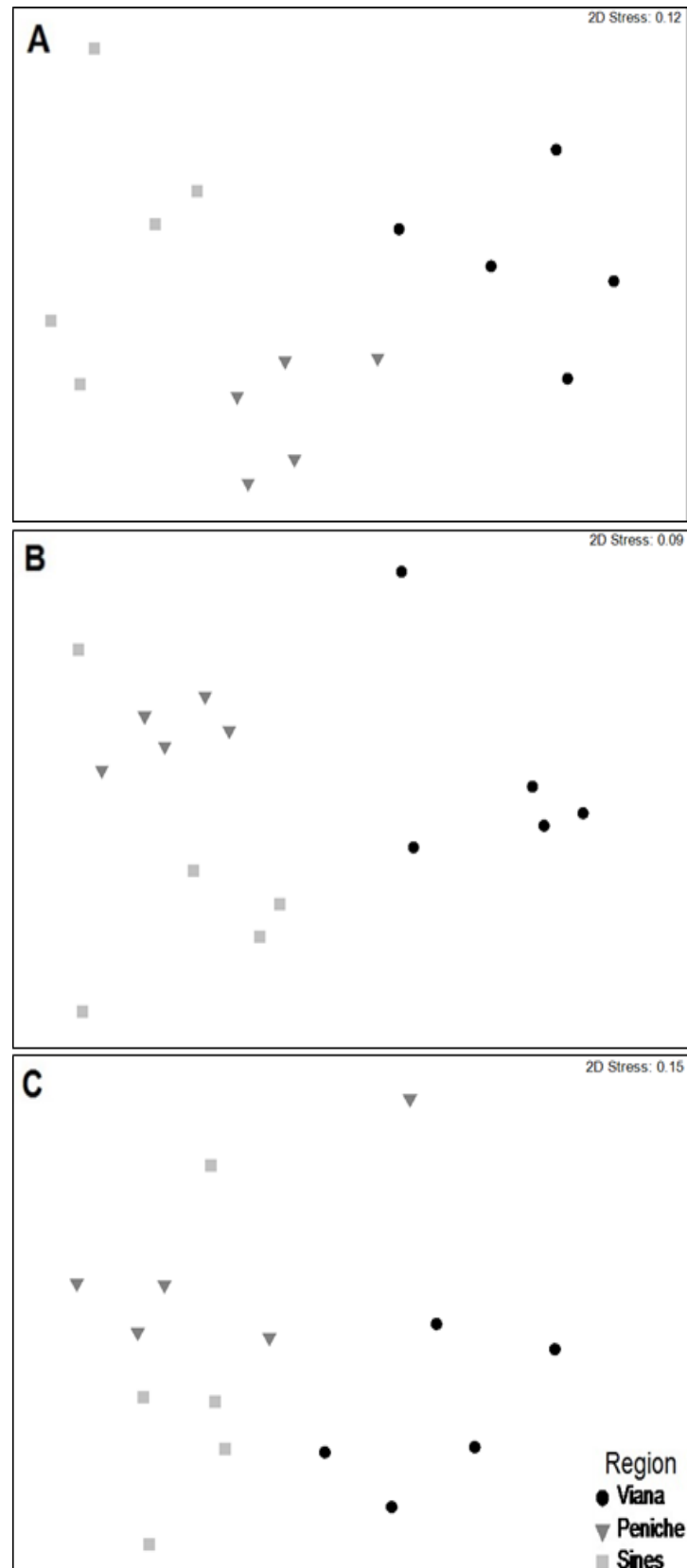


Figure 6: Two-dimensional non-metric multidimensional scaling plot showing similarities in the structure of algal assemblages between centroids of reefs within each region over the three sampling years (A: 2011; B: 2012; C: 2013).

The richness of algal taxa increased from north to south, presenting significant differences between each region and the others (Tab. 2 and Fig. 7). Species evenness did not show significant differences at all (Tab. 2). The total algal biomass, calculated over all replicates from each region, displayed the largest value at VIA, followed by PEN and SIN, which had a similar biomass (Tab. 2 and Fig. 8). The most representative (according to SIMPER) species in each region are listed in Table 3 in the appendix. In addition, two other kelp species, *Phyllariopsis brevipes* and *Saccorhiza polyschides*, were noticeably found mostly at VIA (mean  $\pm$  SE fresh weight of  $4.98 \pm 1.21$  g and  $14.79 \pm 4.00$  g, respectively), being almost absent at PEN ( $0.08 \pm 1.21$  g and  $0.01 \pm 3.00$  g) and SIN ( $0.11 \pm 1.21$  g and  $1.01 \pm 4.00$  g) (see Tab. 5 in the appendix).

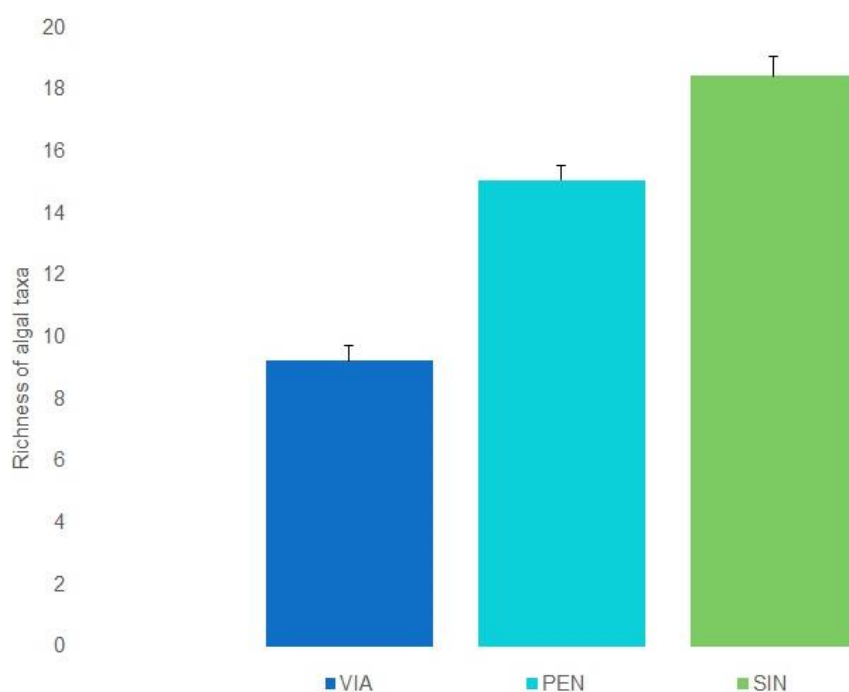


Figure 7: Richness (mean + SE) of algal taxa at each region. Data averaged across six quadrates, 5 reefs and three times. Abbreviations as in Fig. 2.

Source of variation		Total richness of algal taxa			Pielou's evenness index		Total algal biomass	
		df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time	= T	2	1012.07	17.66 ***	0.19	2.83	9.60	5.22 **a
Region	= R	2	1950.86	108.96 ***	0.08	0.56	12.03	6.54 **a
T x R		4	17.90	0.31	0.14	2.02	2.28	1.24 <sup>a</sup>
Reef (TxR)		36	57.30	4.41 ***	0.07	3.17 ***	1.79	4.70 ***
Residual		225	12.99	0.02	0.38			
Cochran's <i>C</i> test			C = 0.122, p<0.01		C = 0.010, p<0.05		C = 0.087, p>0.05	
Transformation			None		None		Ln(x)	
SNK test: Region			SIN > PEN > VIA				VIA > PEN = SIN	
			S.E. = 0.435				S.E. = 0.143	

<sup>a</sup> tested over the pooled term (= TxR + Reef(TxR)); MS<sub>Pooled</sub> = 1.83 with 40 df

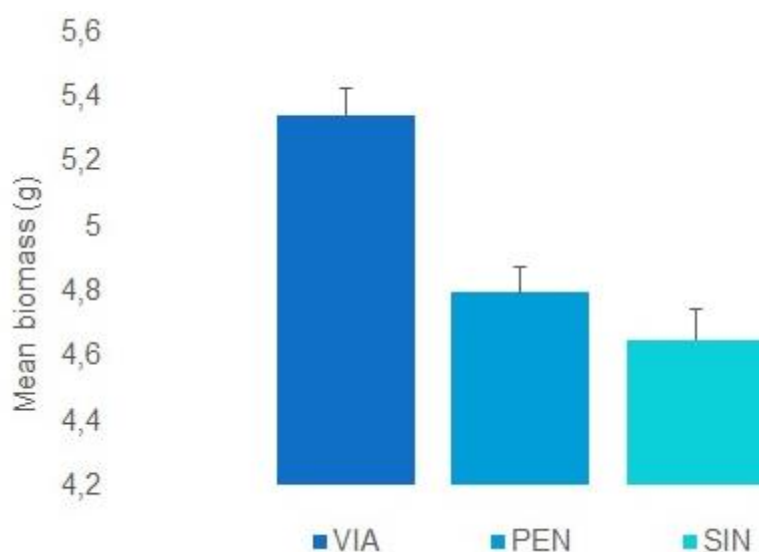


Figure 8: Biomass (mean + SE) of algal taxa at each region. Data averaged across six quadrates, 5 reefs and three times. Abbreviations as in Fig. 2.

Three species (*Laminaria hyperborea*, *Peyssonelia harveyana* and *Phyllophora crispa*) showed temporally variable differences in abundance between regions, as indicated by the significant 'Time x Region' interaction (Tab. 4 in the appendix and Fig. 9). *Laminaria hyperborea* was only recorded in VIA in 2012 and 2013, with a progressive decrease in biomass through the years. *Peyssonelia harveyana* was present at SIN in 2013, being very rare in PEN and absent in VIA. This species showed an increasing biomass in SIN from 2012 to 2013. *Phyllophora crispa*, in 2011, had a larger biomass at VIA relative to the other two regions and years.

Four species showed temporally consistent differences between regions (Tab. 4 in the appendix and Fig. 9). In particular, *Dilsea carnosa* only appeared at VIA; *Lithophyllum incrustans* presented a progressively decreasing abundance from PEN to SIN to VIA. The biomass of *Pterosiphonia complanata* was larger at PEN than at the other two regions, where it was minimal; *Sphaerococcus coronopifolius* was only recorded at SIN through the years.

Three species were characterized by temporally variable fluctuations in their biomass, independently of the region (Tab. 4 in the appendix). *Dictyota dichotoma* showed a decrease in biomass from 2011 to 2012, but it recovered in 2013 (Fig. 9). The average biomass of *Plocamium cartilagineum* was similar in 2011 and 2012, while it clearly

decreased in 2013 (Fig. 10). *Rhodomenia pseudopalmata* displayed a larger biomass in 2011 (though mostly present at VIA only) compared to 2012 and 2013 (Fig. 10).

The remaining four species did not shown significant effect besides that of 'Reef' (Tab. 4 in the appendix and Fig. 10), although some regional trends were evident for each of them. *Chondrus crispus* was exclusively found at VIA, with a larger biomass in 2013, intermediate values in 2011 and very low values in 2012. The greater biomass of both *Codium adhaerens* and *Cypropleura ramosa* were collected at VIA in 2011 and, with much lower values, in 2013, while these two species were present with very low to null biomass at all other regions and times. Finally, *Halopteris scoparia* tended to be completely absent in 2011 at each region, while in the other two years it was only found at PEN and SIN, with larger values at the southernmost region, particularly in 2013 (Fig. 10).



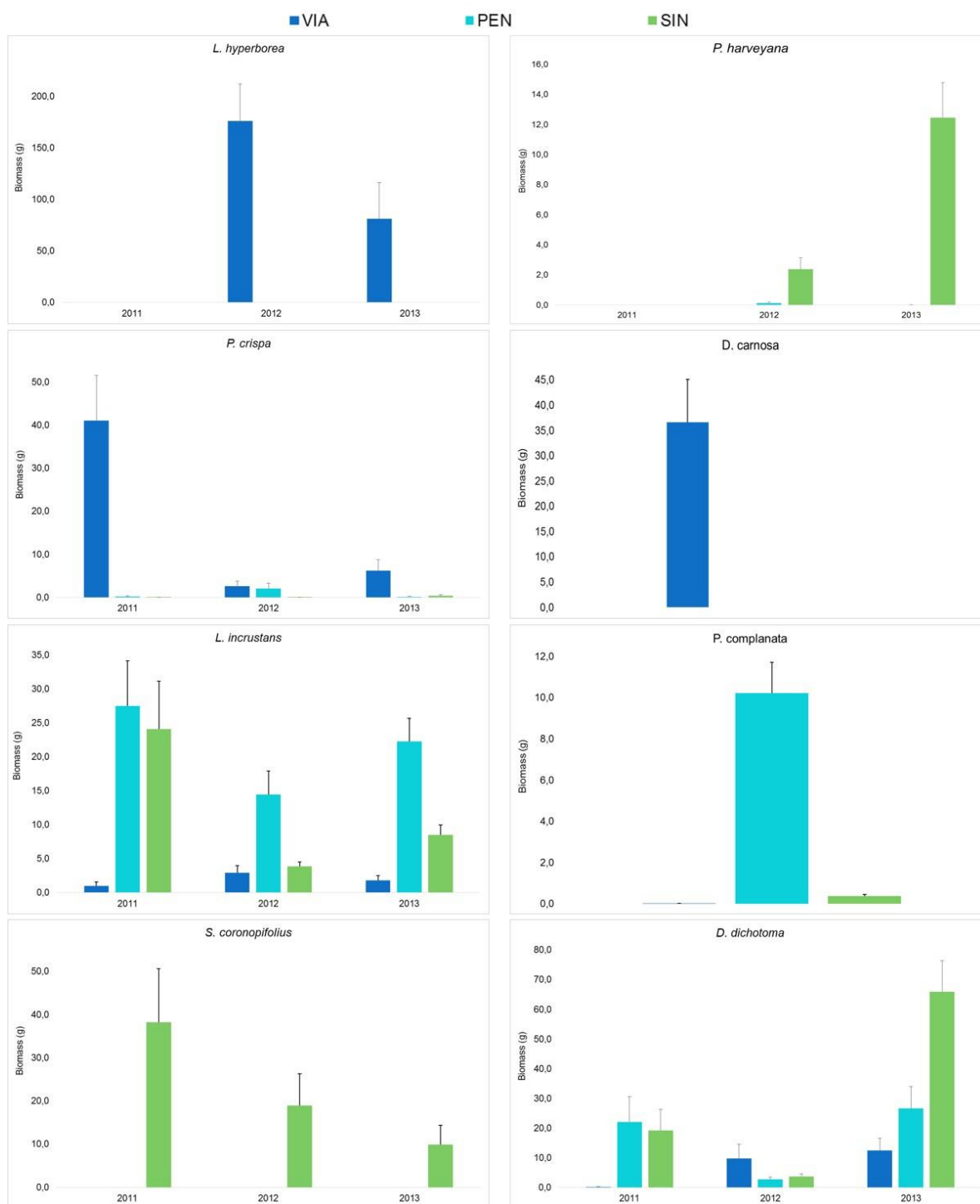


Figure 9: Biomass (mean + SE) of individual algal species at each region and time of sampling. Data averaged across six quadrates and five reefs.

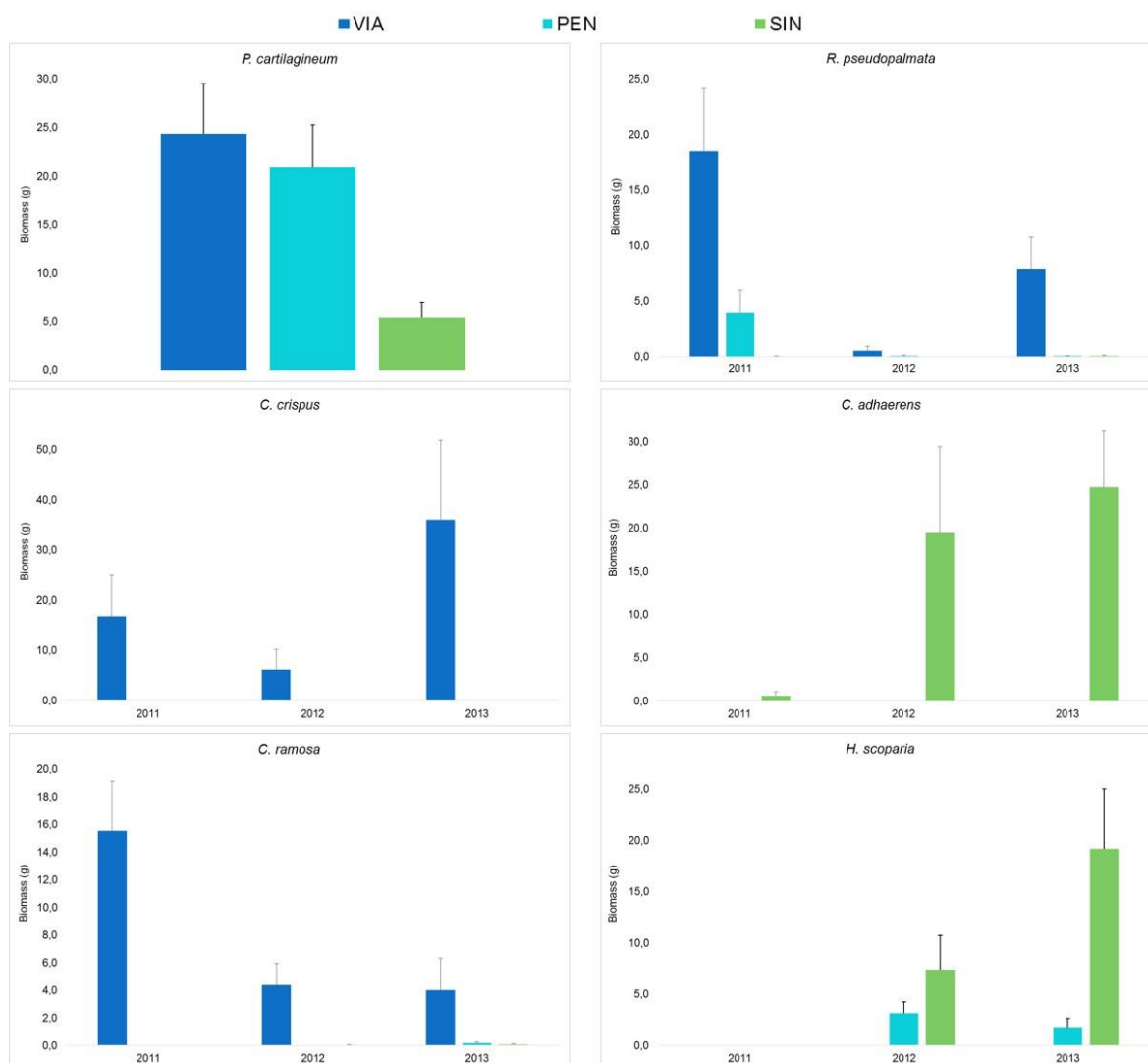


Figure 10: Biomass (mean + SE) of individual algal species at each region and time of sampling. Data averaged across six quadrates and five reefs.

## Discussion

Present findings indicated that the three regions encompassing a latitudinal gradient across continental Portugal differed in the presence and biomass of kelp species and associated macroalgal assemblages, although such differences were not fully consistent over three sampling times spanning a period of two years. Viana do Castelo, located in northern Portugal, was clearly separated from the other two regions in terms of the structure and biomass of macroalgal assemblages, according to previous observations (Tuya *et al.* 2012). This region had the larger algal biomass, but the lowest richness of taxa, in contrast with Sines that had the highest richness and the smallest amount of algal biomass.

The kelp *Laminaria hyperborea* was the most representative species in the assemblages from Viana do Castelo, as expectable according to its affinity for cold water and its southern distribution limit located in the north of the Iberian Peninsula (Pérez-Ruzafa *et al.* 2003). Analogously, other species, such as *Dilsea carnosa* and *Phyllophora crispa*, which have a boreal distribution in the Atlantic and reach their southernmost populations in continental Europe at the Iberian Peninsula, were also characteristic of the shallow subtidal rocky habitats of Viana do Castelo. Similarly, but in the opposite way, subtidal reefs from Sines were dominated by species either widely distributed or abundant in 'warm' environments, such as the Mediterranean Sea. These included, for instance, *Dictyota dichotoma*, *Codium adhaerens* and *Sphaerococcus coronopifolius*.

The overall latitudinal gradient in ocean climate, e.g. decreasing Chl *a* concentration and increasing SST, from North to South Portugal seems to be connected with the distribution of macroalgal subtidal assemblages. For example, the occurrence of large, highly productive, algal species, such as kelps, at Viana do Castelo would be consistent with this model, in spite of the relatively lower value of richness of taxa in north Portugal. In fact, kelp species hold a 38.4 % of the overall biomass from reefs at Viana do Castelo. The rate of reproduction of kelp species of the order Laminariales, in particular, is negatively affected by high temperatures and reduced availability of nutrients (Bartsch *et al.* 2008; Pereira *et al.* 2011) and such response could be responsible, at least in part, for the larger presence of kelps at Viana do Castelo compared to the other regions. In addition, a cold-water 'pocket' spanning north Portugal (including the Viana do Castelo region) and south Galicia has long been recognized as having an important influence on marine biota along this coastal stretch (Southward *et al.* 1995; Peliz and Fiúza 1999), leading to hypothesize that the abundance of kelps would decrease moving southward in parallel with the

increase of ocean temperature. Nevertheless, empirical evidence of such latitudinal decrease in kelp abundance is scarce in the present region, except some recent works (Tuya *et al.* 2012; Assis *et al.* 2013), as well as along other temperate coasts worldwide (Merzouk and Johnson 2011).

Although cause-effect relationships cannot be specifically unravelled by our data and non-manipulative approach, the documented regional pattern in the distribution of kelp is consistent with the general decrease in the intensity of upwelling events in this geographic area since 1941, which has been responsible for increased temperatures and reduced nutrient availability off Portuguese coastal waters (Lemos and Pires 2004). This is another mechanism, not mutually exclusive relative to the previously discussed, that may have negatively affected the presence of kelps across continental Portugal during the last decades. Moreover, such oceanographic patterns could be exacerbated by the presence of the Nazaré Canyon (39.6° N), extending across the Portuguese continental margin from the coast to abyssal depths down to 4500 m (Slagstad and Wassmann 2001). This canyon represents a geographical discontinuity between Peniche and Sines in the south and Viana do Castelo in the north (Tuya *et al.* 2012). Large extensions of sandy bottoms between Viana do Castelo and the southern regions, would also act as physical barriers, since these habitats are unsuitable for most seaweeds.

Interestingly, in the present study, only three kelp species (*Laminaria hyperborea*, *Phyllariopsis brevipes* and *Saccorhiza polyschides*) out of the total seven described for the Portuguese coast, including one exotic from Japan (Rodrigues 1963; Araújo *et al.* 2003), were found. This could represent additional evidence of the decline of kelps along the Portuguese coast. Such three species were, by far, more abundant at VIA than at PEN and SIN (as obvious, however, for *L. hyperborea* which has its southern limit of distribution in north Portugal), analogously to *Laminaria ochroleuca* reported by Tuya and co-workers (2012), but not in the present study. According to their potential role as habitat-formers, it might be expected a positive relationship between the abundance of kelps and the richness of associated taxa, though such association might be stronger for fauna than for algae, which could compete more with canopy-forming species for resources, such as space (e.g. Maggi *et al.* 2012). Instead, the opposite pattern occurred in this study, with a progressively increasing richness moving south as long as kelps decreased. This suggests that, in the study system, diverse macroalgal assemblages can be maintained also independently of the presence of kelp species. Such situation could be explained by the fact that the flora of transitional areas, such as PEN, may include taxonomic elements from

different climate regions, being characterized by a larger diversity compared to that from the northern region.

Despite the very limited available amount of quantitative data on subtidal macroalgal assemblages in Portugal, there is a perception by local and scientific communities that the abundance and distribution of kelps have been reduced in the last decades (Assis *et al.* 2009). Such trend may have negative consequences at several levels as kelps are among the most productive ecosystems worldwide, directly support a relevant component of coastal biodiversity, provide structurally complex habitats for organisms targeted by commercial fisheries, represent a source of food for nearby systems (e.g. sandy beaches) and are exploited as sources of organic fertilizing matter for agriculture and of highly valuable compounds for medicine and the cosmetic industry (see Beaumont *et al.* 2007; Smale *et al.* 2013). Therefore, the knowledge of their ecology, including their patterns of abundance and distribution, is a key requisite to support management and conservation actions aimed at preventing their further reduction and eventually disappearance, with all the associated goods and services, under the predicted increase of natural and anthropogenic pressures. A critical advantage to such knowledge can be provided, particularly in the context of assessments of climate-related effects, by studies, such as the present one, examining shifts in the distribution of species across clear environmental gradients.

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## Appendix

Table 3: SIMPER results outlining the most representative species for each region according to their contribution ( $\delta_i$ ) to within-region dissimilarities.

Species	Avg. biomass	$\delta_i$	$\delta_i\%$	Cumul. $\delta_i\%$
Viana do Castelo				
<i>Laminaria hyperborea</i>	85.67	4.30	33.61	33.61
<i>Dilsea carnosa</i>	36.60	2.25	17.59	51.20
<i>Phyllophora crispa</i>	16.61	1.37	10.75	61.94
<i>Cryptopleura ramosa</i>	7.96	0.77	6.04	67.98
<i>Plocamium cartilagineum</i>	9.53	0.75	5.90	73.89
<i>Chondrus crispus</i>	19.70	0.66	5.15	79.04
<i>Rhodomenia pseudopalmata</i>	8.94	0.57	4.43	83.47
Peniche				
<i>Lithophyllum incrustans</i>	21.40	8.01	32.30	32.30
<i>Plocamium cartilagineum</i>	35.31	7.33	29.54	61.84
<i>Dictyota dichotoma</i>	17.18	2.83	11.43	73.26
<i>Pterosiphonia complatata</i>	10.22	2.42	9.76	83.02
Sines				
<i>Dictyota dichotoma</i>	29.66	4.98	29.08	29.08
<i>Lithophyllum incrustans</i>	12.15	3.71	21.60	50.78

<i>Sphaerococcus coronopifolius</i>	22.33	2.06	12.04	62.83
<i>Plocamium cartilagineum</i>	5.84	1.13	6.61	69.43
<i>Codium adhaerens</i>	14.93	0.94	5.51	74.94
<i>Halopteris scoparia</i>	8.85	0.80	4.69	79.63
<i>Peyssonelia harveyana</i>	4.94	0.64	3.71	83.34

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Table 4: ANOVA examining the effects of time, region and reef on the most representative species for each region. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . Denominators for F as in Table 1.

		<i>Chondrus crispus</i>			<i>Codium adhaerens</i>		<i>Cryptopleura ramosa</i>		<i>Dictyota dichotoma</i>	
Source of variation		df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time	= T	2	2295.25	0.75	1604.36	2.01	418.81	1.8	20950.31	5.69**
Region	= R	2	11638.96	5.07	6688.19	4.17	1878.44	4.33	11130.59	1.34
T x R		4	2295.99	0.75	1604.36	2.01	433.70	1.87	8281.38	2.25
Reef (TxR)		36	3063.31	3.78 ***	797.19	1.89**	232.1	5.18***	3679.26	5.46***
Residual		225	810.40		421.50		44.85		673.61	
Cochran's C test		C = 0.594, p<0.01			C = 0.476, p<0.01		C = 0.370, p<0.01		C = 0.209, p<0.01	
Transformation		None			None		None		None	

		<i>Dilsea carnosa</i>			<i>Halopteris scoparia</i>		<i>Laminaria hyperborea</i>		<i>Lithophyllum incrustans</i>	
Source of variation		df	MS	F	MS	F	MS	F	MS	F
Time	= T	2	1920.20	0.34	1097.82	1.37	77461.21	3.71	5.41	1.44
Region	= R	2	40197.29	20.93	1997.32	2.24	220169.62	2.84	89.47	16.51*
T x R		4	1920.20	0.34	891.29	1.11	797.19	3.71 *	5.42	1.48
Reef (TxR)		36	5661.08	3.52***	801.00	14.51***	20854.44	3.22***	3.75	5.28***
Residual		225	1608.89		55.19		6479.82		0.71	
Cochran's C test		C = 0.323, p<0.01			C = 0.464, p<0.01		C = 0.332, p<0.01		C = 0.081	
Transformation		None			None		None		Ln(x)	
SNK test		Region					T x R		Region	
		S.E. = 4.619					S.E. = 26.365		S.E. = 0.238	
		VIA>PEN=SIN					2011: VIA=PEN=SIN		PEN>VIA=SIN	
							2012: VIA>PEN=SIN			
							2013: VIA>PEN=SIN			

*Peyssonelia harveyana*      *Phyllophora crispa*      *Plocamium cartilagineum*      *Pterosiphonia complanata*

Source of variation		df	MS	F	MS	F	MS	F	MS	F
Time	= T	2	435.16	8.86***	4221.88	8.05 **	9166.51	3.54 *	186.23	0.6
Region	= R	2	725.77	1.66	7811.24	1.66	23201.88	5.43	3017.30	19.06 **
T x R		4	437.97	8.91***	4691.49	8.96 ***	4276.12	1.65	158.29	0.51
Reef (TxR)		36	49.13	3.14***	523.55	1.39	2589.01	2.53 ***	308.4596	11.97 ***
Residual		225	15.64		55.19		1025.02		25.77	
Cochran's C test		C = 0.454, p<0.01		C = 0.536, p<0.01		C = 0.359, p<0.01		C = 0.413, p<0.01		
Transformation		None		None		None		None		
SNK test		T x R		T x R				Region		
		S.E. = 1.278		S.E. = 4.175				S.E. = 1.325		
		2011: VIA=PEN=SIN		2011: VIA>PEN=SIN				PEN>VIA=SIN		
		2012: VIA=PEN=SIN		2012: VIA=PEN=SIN						
		2013: SIN>VIA=PEN		2013: VIA=PEN=SIN						

*Rhodymenia pseudopalmata*

*Sphaerococcus coronopifolius*

Source of variation		df	MS	F	MS	F
Time	= T	2	1223.35	3.37 *	2096.38	0.72
Region	= R	2	2084.61	3.08	14957.60	7.13 *
T x R		4	677.22	1.87	2096.38	0.72
Reef (TxR)		36	362.53	3.11 ***	2912.79	6.94 ***
Residual		225	1164.42			
Cochran's C test		C = 0.4140, p<0.01		C = 0.4852, p<0.01		
Transformation		None		None		
SNK test				Region		
				S.E. = 4.826		
				SIN>VIA=PEN		

Table 5: Taxa distribution per region and climate affinity (C.A.: I, warm-water; II, cold-water; III, widely distributed).

	Viana do Castelo		Peniche		Sines		C. A.
	Mean biomass (g)	S.E.	Mean biomass (g)	S.E.	Mean biomass (g)	S.E.	
Chlorophyta							
<i>Cladophora pellucida</i>			0.1100	0.09	0.4300	0.09	I
<i>Cladophora</i> sp.			0.1000	0.03	0.1400	0.03	III
<i>Cladophora</i> spp.			0.0100	0.02	0.0700	0.02	III
<i>Codium adhaerens</i>					14.9300	2.77	I
<i>Codium tomentosum</i>			0.4261	0.02	4.2672	1.38	III
<i>Codium vermilara</i>			4.2494	1.97	10.5543	3.53	III
Filamentous (undetermined)			3.3900	1.97	0.6300	0.13	III
<i>Monostroma grevillei</i>			0.0001	0.19	0.6800	0.19	III



<i>Ulva clathrata</i>	0.0439	0.03					III
<i>Ulva lactuca</i>					<0.0001	0.00	III
<i>Ulva rígida</i>	0.0416	0.02	0.0076	0.02			III
<i>Ulva</i> sp.	0.0006	0.00	0.0210	0.02	0.0557	0.02	III
Rhodophyta							
<i>Acrosorium ciliolatum</i>	0.0142	0.23	6.1208	1.13	0.0427	1.13	III
<i>Acrosorium venulosum</i>	0.4300	0.25	0.7600	0.31	0.0100	0.31	III
<i>Aglaothamnion byssoides</i>			0.0083	0.01			III
<i>Aglaothamnion</i> sp.			0.0500	0.03	0.0100	0.03	III
<i>Ahnfeltiopsis devoniensis</i>	0.0014	0.00					II
<i>Ahnfeltia plicata</i>	<0.0001	0.00					II
<i>Anotrichium furcellatum</i>			0.0003	0.00	0.0009	0.00	III
<i>Asparagopsis armata</i>			64.77	10.29	4.72	10.30	III
<i>Apoglossum ruscifolium</i>			<0.0001	0.00	<0.0001	0.00	III

<i>Bonnemaisonia asparagoides</i>			0.2600	0.13	0.4000	0.10	III
<i>Bornetia secundiflora</i>			0.0700	0.04	0.0100	0.04	I
<i>Bornetia</i> spp.					<0.0001	0.00	I
<i>Calliblepharis ciliata</i>	9.5259	2.27	0.0021	2.25			II
<i>Ceramium ciliatum</i>			0.1100	0.08	0.1300	0.08	III
<i>Ceramium echionotum</i>					0.0006	0.00	III
<i>Ceramium virgatum</i>	0.0064	0.00	0.0001	0.00			II
<i>Ceramium</i> sp			0.0103	0.01			III.
<i>Ceramium</i> spp.	0.0001	0.11	0.0197	0.11	0.5714	0.11	III
<i>Champia parvula</i>			0.0670	0.02	0.0511	0.02	III
<i>Chondracanthus acicularis</i>	1.2210	0.29	0.4964	0.30	0.3809	0.30	III
<i>Chondracanthus teedei</i>	1.9479	0.53	0.0003	0.46	0.0110	0.46	III
<i>Chondria scintillans</i>	0.2499	0.12					
<i>Chondria coerulescens</i>	2.3212	1.32	0.0532	0.03			III
<i>Chondria dasyphylla</i>	4.3767	1.40	0.3038	1.40	0.4020	1.40	III

<i>Chondrus crispus</i>	19.6974	4.17			0.0012	3.76	II
<i>Corallina officinalis</i>	0.3348	0.23	2.7873	1.63	0.7362	1.63	III
<i>Corallina elongata</i>			0.3000	0.48	3.6100	0.55	III
<i>Cordylecladia erecta</i>	0.0793	0.03					III
<i>Cryptonemia lomation</i>	2.3459	0.93					I
<i>Cryptopleura ramosa</i>	7.9553	1.14	0.0509	0.64	0.0339	0.64	III
<i>Drachiella heterocarpa</i>					0.0253	0.01	II
<i>Drachiella spectabilis</i>	0.7820	1.22	0.0057	0.22			II
<i>Drachiella</i> spp.			0.0100	0.01			II
<i>Dilsea carnosia</i>	36.6047	5.86					II
<i>Dudresnaya verticillata</i>					0.0018	0.00	III
<i>Erythroglossum laciniatum</i>	7.4949	1.48	0.0253	1.48	0.0001	1.48	III
<i>Falkenbergia rufolanosa</i> phase			0.40	0.33	1.23	0.30	I
<i>Gayliella flácida</i>			0.0012	0.00			III
<i>Gelidium corneum</i>	9.1889	3.32	0.1090	3.32			III

<i>Gelidium pusillum</i>			0.0100	0.00			III
<i>Gelideae</i> spp.	0.4839	0.00	<0.0001	0.00			III
<i>Gracilaria multipartita</i>	0.1371	0.09					I
<i>Griffithsia</i> sp.					0.0001	0.00	III
<i>Griffithsia</i> spp.			0.1116	0.04	0.0367	0.01	III
<i>Gymnogongrus crenulatus</i>	1.2652	0.31	0.0200	0.18	0.0051	0.18	I
<i>Kallymenia reniformis</i>	0.5956	0.17	0.0002	0.17			III
<i>Halopithys incurva</i>			0.4500	0.14			I
<i>Halurus equisetifolius</i>			0.1511	0.03	0.0052	0.03	III
<i>Heterosiphonia plumosa</i>	0.7729	0.42	0.8528	0.16	0.0388	0.13	II
<i>Hypoglossum hypoglossoides</i>	0.9278	0.18	0.0194	0.17	0.0001	0.17	III
<i>Jania rubens</i>	0.0008	0.17	0.8999	0.18	0.4518	0.18	III
<i>J. rubens</i> var. <i>corniculata</i>					0.0221	0.01	I
<i>Liagora distenta</i>					0.0234	0.01	I
<i>Liagora víscida</i>					0.0016	0.00	I

<i>Lithophyllum incrustans</i>	1.9126	2.49	21.3972	2.58	12.1498	2.10	III
<i>Lomentaria articulata</i>	0.0733	0.03					III
<i>Lomentaria clavellosa</i>			<0.0001	0.00	<0.0001	0.00	III
<i>Lomentaria orcadensis</i>	0.0084	0.00					II
<i>Microcladia glandulosa</i>					0.0037	0.00	III
<i>Monosporus pedicellatus</i>			<0.0001	0.00	<0.0001	0.00	III
<i>Nitophyllum punctatum</i>	0.0007	0.06	0.3757	0.08	0.0793	0.07	III
<i>Osmundea pinnatifida</i>			0.0027	0.00	0.0053	0.00	I
<i>Palmaria palmata</i>	0.1188	0.08					II
<i>Peyssonnelia atropurpurea</i>	0.0739	0.03	0.0142	0.01			III
<i>Peyssonnelia harveyana</i>			0.0448	0.19	4.9408	0.70	III
<i>Peyssonnelia rubra</i>			0.4000	0.14			III
<i>Phyllophora crispa</i>	16.6109	2.77	0.8140	0.70	0.1557	0.70	II
<i>Phyllophora sícula</i>	0.4800	0.31					III
<i>Plocamium cartilagineum</i>	9.5268	4.48	35.3076	4.48	5.8370	3.17	III

<i>Plumaria plumosa</i>	0.0002	0.00					III
<i>Polyneura bonnemaisonii</i>	0.2300	0.08					III
<i>Polysiphonia denudata</i>	0.5696	0.21	0.3241	0.21	0.0582	0.21	III
<i>Polysiphonia fucoides</i>	0.0034	0.00					II
<i>Polysiphonia nigra</i>			0.0010	0.00			III
<i>Polysiphonia</i> sp.	<0.0001	0.01	0.0300	0.01	0.0100	0.01	III
<i>Polysiphonia</i> spp.	0.0300	0.15	<0.0001	0.15	1.1400	0.20	III
<i>Pterosiphonia ardreana</i>	0.1194	0.07	0.3984	0.09	0.0039	0.09	II
<i>Pterosiphonia complanata</i>	0.0162	0.67	10.2170	1.11	0.3695	1.00	I
<i>Pterosiphonia parasítica</i>			0.0500	0.01	<0.0001	0.00	III
<i>Pterosiphonia pennata</i>	0.0052	0.00	0.0259	0.02			I
<i>Pterosiphonia</i> spp.	0.7207	0.25	0.3556	0.10			III
<i>Pterothamnion plúmula</i>	0.6817	0.36	0.0001	0.00			II
<i>Pterothamnion crispum</i>			<0.0001	0.00	<0.0001	0.00	I
<i>Pterothamnion</i> spp.			<0.0001	0.00	<0.0001	0.00	III

<i>Radicilingua thysanorhizans</i>			<0.0001	0.00			I
<i>Rhodophyllis divaricata</i>			0.0800	0.04	<0.0001	0.04	III
<i>Rhodymenia holmesii</i>	7.4716	1.29	0.4313	1.29	0.0733	1.29	I
<i>Rhodymenia pseudopalmata</i>	8.9422	1.59	1.3316	0.84	0.0334	0.70	III
<i>Scinaia furcellata</i>	0.0519	0.03					III
<i>Sphaerococcus coronopifolius</i>					22.3300	3.55	III
<i>Sphondylothamnion multifidum</i>	0.3200	0.13	<0.0001	0.00	<0.0001	0.00	III
Ochrophyta							
<i>Carpomitra costata</i>			0.0038	0.00			I
<i>Cladostephus spongiosus</i>			0.5634	0.28	0.0872	0.28	III
<i>Colpomenia peregrina</i>			0.0028	0.00			III
<i>Cystoseira baccata</i>			0.5100	0.15			III
<i>Cystoseira tamariscifolia</i>			0.0957	0.04			I
<i>Cystoseira nodicaulis</i>					0.2608	0.07	I
<i>Cystoseira</i> sp.					0.0506	0.02	III

<i>Cutleria adspersa</i>					0.0917	0.04	I
<i>Desmarestia aculeata</i>	0.2542	0.17					II
<i>Desmarestia ligulata</i>	0.1200	0.06	<0.0001	0.04			II
<i>Dictyopteris membranacea</i>	0.5489	0.14	0.0298	0.10	0.0299	0.10	III
<i>Dictyota dichotoma</i>	7.4766	2.87	17.1831	3.29	29.6606	4.04	III
<i>Ectocarpales</i>			0.0100	0.01	3.1700	2.07	III
<i>Halopteris filicina</i>			0.7092	1.96	7.9744	1.95	I
<i>Halopteris scoparia</i>			1.6400	0.83	8.8500	1.63	III
<i>Laminaria hyperborea</i>	85.6679	12.74					II
<i>Petalonia fáschia</i>			0.0098	0.01			III
<i>Phyllariopsis brevipes</i>	4.9754	1.21	0.0780	1.21	0.1141	1.21	I
<i>Ralfsia verrucosa</i>			0.1700	0.28	1.0300	0.28	III
<i>Saccorhiza polyschides</i>	14.7894	4.00	0.0087	3.00	1.0123	4.00	II
<i>Sargassum vulgare</i>					0.1210	0.06	I
<i>Spatoglossum solieri</i>			0.0307	0.02	0.1384	0.04	I



<i>Taonia atomaria</i>			0.1100	0.50	2.5700	0.50	III
<i>Zanardinia prototypus</i>	3.6671	1.10	2.1978	1.13	0.3731	1.13	I
Total biomass	274.3143		182.5749		147.4452		
Number of taxa							
I	10		18		21		
II	18		10		6		
III	36		64		55		
Total number of taxa	64		92		82		
Percentage (%)							
I	15.6		19.6		25.6		
II	28.1		10.9		7.3		
III	56.3		69.6		67.1		

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